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Inducing Ametropias in Hatchling Chicks by Defocus—Aperture Effects and Cylindrical Lenses

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Light-weight translucent plastic goggles with convex or concave rigid contact lens inserts were applied unilaterally to the eyes of young chicks. Convex and concave cylindrical lenses produced astigmatic refractive errors. The magnitude of the induced astigmatism was less than that of the inducing lens and varied with axis orientation. Decreased aperture size or interruption of the defocus resulted in a decreased response to refractive defocus. Slit apertures and spherical defocus produced variable amounts of myopia, hyperopia and astigmatism. Choroidal changes (increased thickness) were observed only in birds developing hyperopia or recovering from myopia.

Chick Defocus Astigmatism Aperture size Aperture shape

INTRODUCTION

For the past two decades, efforts to manipulate the refractive development of the eye have concentrated on form deprivation experiments in which early visual experience is degraded by suturing the eyelids together or by using a goggle which diffuses the light entering the eye. Generally speaking, such work has led to the development of induced myopia, whether carried out with mammals (Wiesel & Raviola, 1977; Tigges, Tigges, Fernandes, Eggers & Gammon, 1990; Sherman, Norton & Casagrande, 1977; McBrien & Norton, 1992; O'Leary & Millodot, 1979) or with birds (Wallman, Turkel & Trachtman, 1978; Pickett-Seltner, Sivak & Pasternak, 1988). More recently, it has been shown that it is possible to manipulate the early refractive development of the chick eye in the myopic or hyperopic directions by defocussing the retinal image with convex or concave lenses (Schaeffel, Glasser & Howland, 1988; Sivak, Barrie, Callender, Doughty, Seltner & West, 1990). We have extended this work by exploring the possibility of employing either hydrogel soft contact lenses applied to the eye or rigid contact lenses mounted in a goggle which is applied above the eye of hatchling chicks (Irving, Callender & Sivak, 1991). We found that despite the flexibility of the soft lenses, and the fact that significant amounts of hyperopia and myopia are produced, the normal early refractive development of the chick eye is shifted in the hyperopic direction because of pressure induced corneal flattening. We believe that similar effects have contaminated the results of a variety of studies using either lid suture or direct contact lens application to alter the visual stimulus.

We have used a light-weight plastic goggle with rigid contact lens inserts mounted over the eye to show that the hatchling chick eye will respond accurately to defocus of between −10 and +15 D by developing a refractive error equal in sign and amount to the inducing contact lens (Irving, Sivak & Callender, 1992). Beyond this range there is first a levelling off followed by a decrease in response. Refractive state changes are a result of relative increases and decreases in axial length of the eye, although high levels of hyperopia also involve corneal flattening. Also, astigmatic refractive states can be induced by using concave power cylindrical contact lenses or by reversing the sign of the inducing lens after first producing myopic or hyperopic refractive states. The astigmatic response appears to display a meridional sensitivity.

The study which follows represents an effort to characterize further the response of the hatchling chick eye to astigmatic defocus by examining the response to both concave and convex cylindrical lenses, both in terms of magnitude of the induced astigmatism and the meridional sensitivity of this effect. The effect of aperture size and shape is examined as well as the effects of defocus interrupted by periods of normal visual experience. Finally, we report the results of experiments which examine the possible changes in choroidal thickness associated with development and recovery from defocus induced refractive errors.

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METHODS

All chicks used in these experiments were broilers obtained from a local poultry plant on the day of hatching. The chicks were maintained in stainless steel brooders at an initial temperature of 32°C. They were given food and water *ad libitum*, and were subject to a daily fluorescent light cycle of 14 hr light/10 hr dark. The light period extended from 4:00 a.m. to 6:00 p.m.

Rigid gas permeable single curvature contact lenses, 12.0 mm diameter and 8.1 mm base curvature of various refractive powers were inserted into an aperture in the anterior-lateral zone of a 20 mm dia translucent goggle. The contact lenses were located at a corneal vertex distance of 7.0 mm when the goggle was fixed to the eye. Lens powers reported here take vertex distance into account. The aperture (10 mm diameter) forms an angle of about 70 deg when measured to the corneal vertex.

The goggle–lens combination was fixed unilaterally to the eye by means of velcro rings around the base of the goggle and on the feathers around the eye. This made it possible to remove the goggle–lens combination for periodic cleaning and ocular measurement. The chicks showed no behavioural sign of wearing the device.

In vivo ocular measurements of refractive state and corneal curvature were made by retinoscopy and ophthalmometry, respectively, as described previously (Irving *et al.*, 1992). All birds were sacrified by CO_2 asphyxiation after each experiment. Ocular dimensions were measured by A-scan ultrasonography. The eyes were then removed, weighed and measured externally with vernier calipers. Ultrasound and vernier measures were estimated to be accurate to ± 0.05 mm. In addition, ocular dimensions, in particular choroidal thickness, were measured from frozen sections of the head and eyes. This approach involved rapidly freezing the head (minus the lower jaw) in a mixture of acetone and dry ice and sectioning it on a freezing microtome. As microtome sections of head (and eyes) were removed, the remaining block of tissue was photographed from above with a camera and bellows. Photographic negatives showing the greatest lens thickness were assumed to represent axial sections of the eye. Unless otherwise stated all results are expressed as the difference between the treated and control eyes.

Experiment 1—astigmatic defocus

Cylindrical contact lenses (plano/-9 D, $N=23$; plano/$+10$ D, $N=16$) were applied unilaterally to the eyes of 39 chicks at various axes (45, 90, 135 and 180 deg) relative to the palpebral fissure (Fig. 1). The lenses were applied either on the day of hatching ($N=33$ because it was felt that the effects would be greatest when applied at hatching) or 2 days after hatching ($N=6$ because better measures of corneal curvature can be obtained on slightly older birds particularly in the vertical meridian). For all of the birds, refractions were measured on the day of hatching, the day of lens application and the day the birds were sacrificed. For 15 of the birds wearing plano/-9 D (axes 180 and 90 deg) refractions were measured daily.

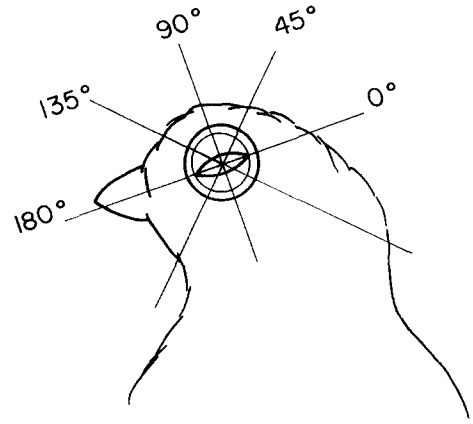

FIGURE 1. Diagram illustrating the orientation of the various meridians relative to the palpebral fissure of the left eye of a chicken.

Corneal curvatures were measured on the day of lens application and the day the birds were sacrificed.

Experiment 2—aperture size and shape

Forty-five birds were divided into three groups of 15 and treated with $+10$ D, -10 D, or plano lenses unilaterally. Each group was subdivided into three groups of five and treated with three different diameters of circular aperture: 10, 5 and 2.5 mm. Aperture size was controlled by varying the size of the opening cut into the translucent goggle. Data were also collected for 13 birds wearing unilateral translucent goggles with no aperture. Eighteen birds were divided into two groups of nine and fitted unilaterally with $+10$ D or -10 D lenses limited by a 3×10 mm slit. The slit was oriented with the long axis perpendicular to the palpebral fissure (90 deg) in one group and obliquely (45 deg) in the other group (Fig. 1). Refractive and corneal curvature measurements were made on all the birds on days 0 and 7. Ocular dimensions and wet eye weights were measured after the birds were sacrificed at 1 week.

Experiment 3—interrupted defocus

Six chicks, three with $+10$ D lenses and three with -10 D lenses, were raised for 1 week. The goggles were removed for 1 hr each morning between 10:00 a.m. and 12:00 p.m. Refractive states were measured daily during the period of lens removal. After 1 week of lens wear the birds were refracted, sacrificed, axial lengths were measured by ultrasonography, the eyes were removed from the head, axial length and equatorial diameter were measured by vernier calipers and the excised eyes were weighed.

Experiment 4—choroid

Corneal curvature and refractive states were measured for 22 chicks on the day of hatching. The chicks were then fitted unilaterally with $+10$ D, -10 D or plano lenses. Two days after hatching the birds were refracted, corneal curvatures were measured, and axial lengths were determined by ultrasonography. The birds were then killed and frozen sections taken of the head. Axial length, axial and equatorial choroidal thickness, and equatorial

diameter were determined from the frozen section photographs.

Goggles containing convex (+10 D), concave (−10 D) and plano lenses in the lateral region of the goggle were applied unilaterally on the day of hatching to the eyes of 11 chicks. After 1 week of lens wear the goggles were removed and the chicks were kept for 1 more day. The birds were refracted and corneal curvatures were measured before the goggles were applied, immediately after the goggles were removed and before the birds were killed. Axial lengths were measured by ultrasonography immediately after the goggles were removed and again immediately before the birds were killed. After the birds were sacrificed frozen sections were taken of the head as described previously. Axial length, axial and equatorial choroidal thickness, and equatorial diameter were measured from photographs of the frozen sections.

RESULTS

Experiment 1—astigmatic defocus

There was no significant difference in refractive error or corneal curvature between the right and left eyes of the birds on the day of application of cylindrical contact lenses; nor was there any significant corneal or refractive astigmatism.

Concave cylindrical inducing lenses (plano/−9 D) produced variable amounts of astigmatic refractive errors (means for different orientations ranged from 2.25 to 5.75 D), with the axis of the induced astigmatism coincident with the axis of the inducing lens. The magnitude of the astigmatism produced was greatest (mean and SD = 5.75 ± 1.50 D) when the plano meridian was placed at 45 deg relative to the palpebral fissure and least (2.25 ± 1.00 D, 2.25 ± 1.50 D) when the plano meridian was along 135 or 180 deg. For the plano/+10 D cylindrical lenses the amount of astigmatism produced also varied with axis of the inducing lens; and the axis of the induced astigmatism coincided with the axis of the inducing lens. The magnitude of the astigmatism was greatest (3.75 ± 2.50 D) when the plano meridian (+10 D) was placed at 135 deg relative to the palpebral fissure and least (1.00 ± 1.50 D) when the plano meridian was at 45 deg relative to the palpebral fissure (Table 1).

The cornea was found to be toroidal, with the flattest principal meridian coincident with the meridian of least myopia. The results for both plano/−9 D and plano/+10 D inducing lenses show corneal astigmatic dioptric values that are about one-half the measured refractive astigmatism (Table 1). In addition to the astigmatic changes, all eyes treated with cylindrical lenses having minus in the power meridian show an overall moderate shift toward myopia. For example, the average refractive error for the plano inducing meridian shows 1.75 ± 1.00 D more myopia than the control eye. The opposite is true for lenses having plus in the power meridian. In this case the average refractive error for the plano meridian is 3.00 ± 1.25 D more hyperopic than the control eye. The algebraic average of the two principal meridians for all orientations are consistently in the range of moderate myopia (3.50 ± 0.50 D) for plano/−9 D lenses and moderate hyperopia (4.25 ± 1.00 D) for the plano/+10 D lenses. It is difficult to separate the astigmatic response from the overall spherical response in terms of differentiating between the axial and corneal changes. The eyes treated with minus power cylindrical lenses were significantly heavier (0.035 ± 0.024 g; $t = 6.99$, d.f. = 22, $P < 0.001$) and larger, both axially (0.23 ± 0.26 mm; $t = 4.24$, d.f. = 22, $P < 0.001$) and equatorially (0.17 ± 0.16 mm; $t = 5.00$, d.f. = 22, $P < 0.001$) than the untreated eye. There was no significant difference in anterior chamber depth between the treated and untreated eyes. Lenses of eyes treated with concave cylindrical lenses were found to be significantly thicker than those of the untreated eyes (0.13 ± 0.17 mm; $t = 3.54$, d.f. = 22, $P < 0.001$). There were no significant differences with respect to orientation. The eyes treated with convex cylindrical lenses were significantly shorter axially (0.26 ± 0.29 mm; $t = 3.43$, d.f. = 14, $P < 0.005$). There were no significant differences in equatorial diameter, wet weight, anterior chamber depth or lens thickness.

Experiment 2—aperture size and shape

Size. There was no difference in refractive error or corneal curvature between the right and left eyes for any of the treatment groups before the goggles were applied. After 7 days of lens wear there was no difference between the right and left eyes of birds treated with plano lenses

TABLE 1. Refractive and corneal astigmatism (mean ± SD) for the right and left eyes of chicks treated for seven days with goggles containing cylindrical lenses applied unilaterally at various axes

Lens			Refractive astigmatism		Corneal astigmatism		
Power	Axis (deg)	N	Control H−V (D)	Treated A−P (D)	Control H−V (mm)	Treated A−P (mm)	Treated A−P (D)
Plano/−9.00 D	45	4	0.00 ± 0.00	+5.75 ± 1.50	+0.02 ± 0.03	+0.08 ± 0.06	+2.75
	90	8	−0.25 ± 0.25	+3.00 ± 2.00	−0.03 ± 0.03	+0.04 ± 0.05	+1.50
	135	4	0.00 ± 0.00	+2.25 ± 1.00	0.00 ± 0.00	+0.02 ± 0.03	+0.75
	180	7	−0.00 ± 0.25	+2.25 ± 1.50	0.00 ± 0.02	+0.00 ± 0.04	0.00
Plano/+10.00 D	45	4	−0.25 ± 0.50	−1.00 ± 1.50	−0.01 ± 0.01	0.00 ± 0.03	0.00
	90	4	−0.25 ± 0.25	−2.25 ± 3.00	−0.02 ± 0.02	−0.03 ± 0.08	−1.25
	135	3	−0.25 ± 0.25	−3.75 ± 2.50	0.00 ± 0.03	−0.08 ± 0.07	−3.00
	180	4	−0.25 ± 0.50	−3.00 ± 1.75	−0.02 ± 0.02	−0.03 ± 0.03	−1.25

H, horizontal meridian; V, vertical meridian; A, plano (no power) meridian; P, power meridian.

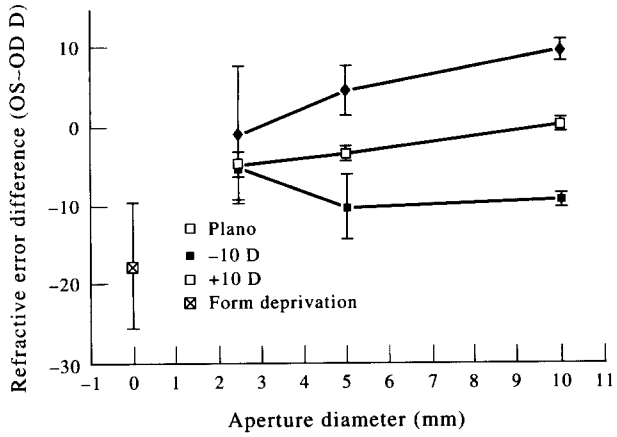

FIGURE 2. Effect of aperture diameter on the refractive error difference between the treated and untreated eyes of chick wearing 10 D convex, 10 D concave and plano lenses for 7 days. The error bars designate the SD.

and 10 mm apertures (-0.00 ± 0.50 D). Those birds wearing plano lenses with 5 and 2.5 mm apertures became significantly (ANOVA $P < 0.001$) more myopic than the control eye (-3.75 ± 0.75 and -5.00 ± 1.50 D respectively). There is a sharp increase in myopia as the aperture size approaches zero (Fig. 2). Translucent goggles with no aperture produce 17.50 ± 8.75 D more myopia in the treated eye than the untreated eye. The difference in refractive error between the treated and untreated eyes of birds treated with 10 mm apertures and +10 and −10 D lenses was very nearly equal to the power of the inducing lenses after 1 week of lens wear. Eyes treated with 5 mm apertures and −10 D lenses became more myopic than the untreated eyes by 10.50 ± 4.25 D while those treated with +10 D lenses became more hyperopic than the treated eyes by only 4.25 ± 3.00 D in the same period. For those birds treated with 2.5 mm apertures the effect of the inducing lenses was decreased for both convex and concave lenses. In fact the mean value (−1.25 D) for those treated with positive lenses was actually more myopic than the control eyes. The variability was high (SD = 8.75 D) and not all birds in this group became myopic. The convergence of the data for +10 and −10 D lenses toward that for plano lenses with decreased aperture size can be seen in Fig. 2. There were no significant differences in corneal curvature, anterior chamber depth or lens thickness for any of the treatment groups. Treated eyes which became hyperopic were shorter than untreated ones, while treated eyes which became myopic were longer (Table 2).

Shape. There was no difference in refractive error between the two eyes for either group of birds before treatment with slit apertures, nor was there any significant astigmatism. After 7 days of lens wear the results for the chicks wearing convex lenses show moderate amounts of hyperopia, large variability and, in one-half of the chicks, moderate amounts of astigmatism. For example, the four chicks wearing +10 D lenses with the slit at 45 deg showed an average hyperopia of $+4.25 \pm 6.75$ D with 2–3 D of astigmatism axis 45 deg in two of the birds. One of the four birds became myopic instead of hyperopic. Similar results were found for the birds treated with +10 D lenses and slits at 90 deg (Table 3). However, in the two chicks with astigmatism (2–3 D) the axis of the astigmatism was at 180 deg. Chicks with concave lenses showed myopia approximately equal to the power of the inducing lenses. Although the variability of these results was greater than those obtained with large circular apertures none of the chicks actually became hyperopic

TABLE 2. Difference in ocular measurements (mean ± SD) between treated and untreated eyes of chicks wearing ± 10 D and plano goggles with various aperture sizes applied unilaterally on the day of hatching

Aperture (mm)	Lens	*N*	Corneal radius of curvature curvature (mm)	Axial length (caliper, mm)	Equatorial diameter (mm)	Wet weight (g)
Day 0						
2.5	+10 D	5	+0.012 ± 0.048			
	Plano	6	+0.006 ± 0.023			
	−10 D	5	−0.016 ± 0.011			
5.0	+10 D	5	+0.019 ± 0.040			
	Plano	6	−0.006 ± 0.022			
	−10 D	5	−0.020 ± 0.031			
10.0	+10 D	5	−0.025 ± 0.036			
	Plano	5	−0.022 ± 0.042			
	−10 D	5	+0.012 ± 0.019			
Day 7						
2.5	+10 D	5	+0.022 ± 0.054	0.00 ± 0.28	+0.02 ± 0.16	+0.017 ± 0.019
	Plano	6	−0.034 ± 0.048	+0.17 ± 0.16	+0.09 ± 0.13	+0.039 ± 0.011
	−10 D	5	0.028 ± 0.034	+0.24 ± 0.16	+0.05 ± 0.25	+0.028 ± 0.029
5.0	+10 D	5	+0.035 ± 0.057	−0.15 ± 0.14	+0.07 ± 0.18	−0.003 ± 0.022
	Plano	6	−0.006 ± 0.092	+0.27 ± 0.10	+0.16 ± 0.11	+0.41 ± 0.016
	−10 D	5	−0.052 ± 0.036	+0.55 ± 0.24	+0.22 ± 0.25	+0.046 ± 0.024
10.0	+10 D	5	+0.019 ± 0.025	−0.08 ± 0.28	+0.04 ± 0.38	−0.006 ± 0.014
	Plano	5	+0.010 ± 0.056	+0.10 ± 0.28	−0.02 ± 0.31	+0.011 ± 0.019
	−10 D	5	−0.010 ± 0.046	+0.32 ± 0.23	+0.28 ± 0.33	+0.042 ± 0.016

TABLE 3. Difference in refractive error and ocular measurements (mean ± SD) between treated and untreated eyes of chicks wearing ±10 D lenses with 3.0 × 10 mm slit apertures applied unilaterally on the day of hatching

Slit orientation (long axis, deg)	Lens	N	Refractive error (average of principle meridians, D)	Corneal radius of curvature (average of principle meridians, mm)	Axial length (caliper, mm)	Equatorial diameter (mm)	Wet weight (g)
Day 0							
45	+10 D	4	+1.00±1.25				
45	−10 D	5	+0.50±0.75				
90	+10 D	4	+0.75±1.50				
90	−10 D	5	+0.00±0.50				
Day 7							
45	+10 D	4	+4.25±6.75	−0.016±0.052	−0.13±0.58	+0.22±0.25	+0.032±0.042
45	−10 D	5	−10.50±5.25	−0.010±0.063	+0.36±0.21	+0.14±0.20	+0.038±0.022
90	+10 D	4	+3.00±3.00	−0.056±0.105	+0.06±0.38	+0.20±0.15	+0.039±0.041
90	−10 D	4	−9.50±1.25	−0.025±0.105	+0.37±0.08	+0.14±0.18	+0.051±0.026

relative to the untreated eye. Moderate amounts of astigmatism were produced in about one-half of the chicks (2–3 D) with a 45 deg axis in all cases. There was no change in the average corneal curvature of the two principal meridians for any of the lens powers or slit orientations. However if one considers only those birds which have refractive astigmatism, the magnitude of the corneal astigmatism agrees very closely with the refractive astigmatism for all lens powers and slit orientations (Table 4). When astigmatism is produced it appears to be mostly corneal. However, corneal astigmatism is always less than refractive astigmatism. Axial length changes were consistent with refractive error changes and there were no differences in anterior chamber depth or lens thickness. There was an increase in equatorial diameter for both positive and negative lenses at both orientations. This results in increased wet weights for positive lenses even though axial length has decreased (Table 3).

Experiment 3—interrupted defocus

After 3 days of lens wear convex lenses produced 4.25±2.00 D of hyperopia relative to the untreated eye, which is approx. 50% of the magnitude of hyperopia produced when the lenses were worn continuously. Concave lenses produce relative myopia of 6.00±1.50 D in the same time period; a value which is similar to that produced with continuous wear. After 1 week of lens wear, refractive errors of the treated eye relative to the untreated eye were +7.00±1.25 and −4.00±3.00 D for convex and concave lenses respectively. Axial length differences were consistent with the sign and magnitude of the refractive errors produced. There were no differences in anterior chamber depth, lens thickness or equatorial diameter. Values for wet weight differences followed the appropraite trend but were not statistically significant.

Experiment 4—choroid

After 2 days of lens wear convex lenses produced +5.75±2.00 D of hyperopia relative to the fellow eye, concave lenses produced −3.50±3.25 D of myopia relative to the fellow eye and there was no difference between the refractive errors of the two eyes of birds treated with plano lenses. There was no difference in corneal curvature measurements, anterior chamber depth, or lens thickness between the treated and untreated eyes for any of the lens powers. Axial lengths of eyes treated with convex lenses were shorter than their fellow eyes and eyes treated with concave lenses were longer than their fellow eyes. Choroidal thickness was not uniform. There was no difference in the axial choroidal regions for any of the lens powers. Eyes treated with convex lenses showed an increase in equatorial choroidal thickness (0.089±0.099 mm) relative to the control eye [Fig. 3(a)]. This was significantly different from treatment with the other two lens (plano and −10 D) powers (Bonferonni t-test, $P<0.05$). There was no difference in equatorial

TABLE 4. Comparison of corneal and refractive astigmatism of the treated eye for chicks in which refractive astigmatism was produced by wearing ±10 D lenses with 3.0 × 10 mm slit apertures applied unilaterally on the day of hatching

Slit orientation (long axis, deg)	Lens	N	Refractive astigmatism (D)	Corneal astigmatism (mm)	Corneal astigmatism (D)
45	+10 D	2	−2.50 × 045	0.057±0.004	−2.00 × 045
45	−10 D	3	−2.75 × 045	0.056±0.016	−2.00 × 045
90	+10 D	2	−2.25 × 180	0.059±0.023	−2.00 × 180
90	−10 D	1	−2.00 × 045	0.038	−1.50 × 045

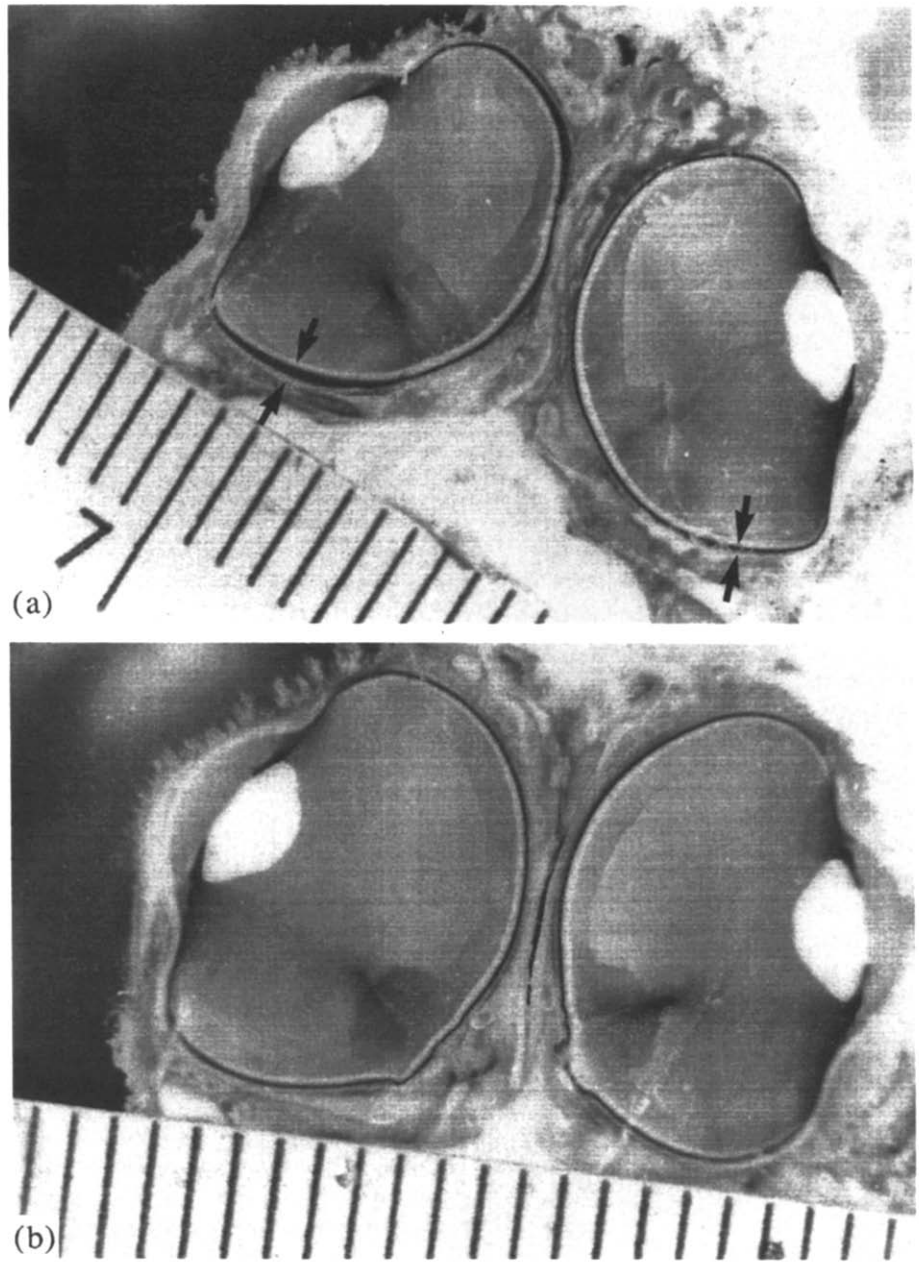

FIGURE 3. Photograph of frozen section of the head and eyes of birds treated unilaterally (left eyes) with 10 D convex (a) or 10 D concave lenses (b) for 2 days showing differences in choroidal thickness (arrows) with convex lens treatment but not with concave lens treatment.

choroidal thickness between the plano and −10 D lens treatments [Fig. 3(b), Table 5].

After 7 days of lens wear, chicks wearing concave lenses became myopic (−8.25±2.50 D) while those wearing convex lenses became hyperopic (+9.50±1.00 D). Myopia and hyperopia decrease by 84% and 40% respectively, 24 hr after lens removal. In birds recovering from myopia, choroidal thickness was significantly increased in all regions by amounts of between 0.07 mm for axial regions and 0.17 mm for equatorial regions. In birds recovering from hyperopia, there was no difference in choroidal thickness between the two eyes (Table 6). Differences between axial lengths measured by ultrasound and by frozen sections (Table 6) reflect in part the choroidal effect.

DISCUSSION

Astigmatism

The developing chick eye can respond to both convex and concave astigmatic defocus. The axis of the induced astigmatism is coincident with the axis of the inducing lens, but the magnitude of the astigmatism is always less than the toricity of the inducing lens. Further, it varies with the orientation of the axis. In the left eye, myopia appears to be most easily produced and hyperopia least easily produced along a meridian 135 deg from the palpebral fissure (Table 1). These experiments indicate that the afferent branch of the loop involved in vision-directed control of ocular development is capable of responding to complex retinal image defocus and that this ability may be preferentially oriented along a

TABLE 5. Difference in refractive error and ocular measurements (mean ± SD) between treated and untreated eyes of chicks wearing goggles with convex, plano and concave lenses applied unilaterally on the day of hatching

Condition	N	Refractive error (D)	Corneal radius of curvature (mm)	Axial length (A-scan, live birds, mm)	Axial choroidal thickness (mm)	Equatorial choroidal thickness (mm)
Day 0						
+10 D	8	−0.50 ± 1.50	−0.008 ± 0.041			
Plano	7	−0.25 ± 0.50	+0.014 ± 0.024			
−10 D	7	−0.00 ± 1.00	−0.016 ± 0.036			
Day 2						
+10 D	8	+5.75 ± 2.00	+0.008 ± 0.029	−0.23 ± 0.26	+0.014 ± 0.032	+0.089 ± 0.099
Plano	7	−0.00 ± 1.50	+0.009 ± 0.014	−0.01 ± 0.15	−0.006 ± 0.010	−0.010 ± 0.017
−10 D	7	−3.50 ± 3.25	−0.003 ± 0.019	+0.13 ± 0.14	−0.003 ± 0.013	−0.020 ± 0.046

particular meridian. This information could be useful in the ongoing search for cellular/molecular components of the local retinal mechanism responsible for this control (Wildsoet & Pettigrew, 1988; Stone, Lin, Laties & Iuvone, 1989). As yet no unusual anatomical or physiological features that correspond to this meridian have been shown but some of the possibilities include; corneal anatomy [avian corneas are tilted slightly nasally (Walls, 1942)], asymmetry in orbital structure or plasticity, correspondence of the preferred meridian with the horizontal or the dominant direction of vergence eye movements when feeding, and a meridian of increased retinal cell density [ganglion cells (Ehrlich, 1981); dopaminergic amacrine cells (Teakle, Wildsoet & Vaney, 1993)]. It is also interesting to note that when astigmatism developed in experiments with spherical lenses [i.e. the reversal experiments (Irving *et al.*, 1992)] and with slit apertures, the most myopic meridian was generally similar to the preferred orientation for development of astigmatism with cylindrical inducing lenses.

The high variability of results obtained with cylindrical inducing lenses is comparable to the increase in variability noted at the convex and concave limits of spherical inducing lenses (Irving *et al.*, 1992), with decreased aperture size or non-circular aperture shape and in the reversal experiments (Irving *et al.*, 1992). All of these conditions represent the limit of accurate compensation. This variability may be the result of corneal curvature variability; a finding which would suggest that the development of the anterior globe is disrupted to a greater extent than that of the posterior globe. The variability of the corneal measurements is high and many of the changes found are not statistically significant for the sample sizes used. However, the most hyperopic meridian corresponds to the flattest corneal meridian. Further, corneal astigmatism is greatest for conditions in which refractive astigmatism is the highest and least for conditions in which refractive astigmatism is the lowest.

Only about one-half of the refractive astigmatism observed with cylindrical inducing lenses can be accounted for by the measured corneal astigmatism. This may be due to a combination of measurement errors (both refractive and corneal) and the fact that the induced refractive error is considerably less than the power of the inducing lenses. However, the fact that the results always indicate a difference in the same direction (corneal astigmatism less than refractive astigmatism) for every bird tested, suggests that the lens contributes to the induced astigmatism. The increase in lens thickness with minus power cylindrical lenses also suggests lenticular

TABLE 6. Difference in refractive error and ocular measurements (mean ± SD) between treated and untreated eyes of chicks wearing goggles with convex, plano and concave lenses applied unilaterally on the day of hatching and removed after 1 week

N	Condition	Refractive error (D)	Corneal radius of curvature (mm)	Axial length (mm)		Equatorial diameter (mm)	Axial choroidal thickness (mm)	Equatorial choroidal thickness (mm)
				A-scan	Frozen section			
Day 0								
3	+10	+0.50 ± 0.50	+0.00 ± 0.03					
3	Plano	+0.75 ± 1.25	−0.01 ± 0.01					
5	−10	−0.75 ± 1.25	+0.01 ± 0.05					
Day 7								
3	+10	+9.50 ± 1.00	+0.06 ± 0.07	−0.35 ± 0.23				
3	Plano	−0.50 ± 0.25	−0.01 ± 0.05	−0.03 ± 0.06				
5	−10	−8.25 ± 2.50	−0.02 ± 0.04	+0.44 ± 0.20				
Day 8								
3	+10	+5.75 ± 2.00	+0.06 ± 0.12	−0.18 ± 0.08	−0.55 ± 0.23	−0.22 ± 0.57	0.00 ± 0.00	+0.03 ± 0.03
3	Plano	−0.25 ± 1.00	−0.01 ± 0.06	−0.15 ± 0.09	−0.23 ± 0.81	+0.30 ± 0.51	0.00 ± 0.02	+0.01 ± 0.03
5	−10	−1.25 ± 1.25	−0.01 ± 0.04	+0.02 ± 0.17	+0.47 ± 0.25 ($n=4$)	+0.42 ± 0.24	+0.07 ± 0.05	+0.17 ± 0.09

involvement. Previous studies (Nathan, Crewther, Crewther & Kiely, 1984; Hayes, Fitzke, Hodos & Holden, 1986; Pickett-Seltner, Weerheim, Sivak & Pasternak, 1987; Troilo, Gottlieb & Wallman, 1987; Sivak, Ryall, Weerheim & Campbell, 1989) have indicated the lens to be isolated from the refractive development of the eye. This point, that is whether lenticular astigmatism does develop, deserves further study.

Astigmatism does not occur in isolation. In all cases where astigmatism results there is also an overall spherical change. For example, the axis meridian also becomes more myopic than the treated eye when the power meridian contains −9 D. It appears that the principal meridians do not develop independently, but a general shift in spherical refraction brings the circle of least confusion onto the retina and astigmatism develops as an attempt at refinement. The same basic argument can be applied to the cases of astigmatism produced with spherical lenses (lens reversal and non-circular aperture shape). In both cases, the spherical refractive shift cannot fully compensate for the induced defocus. Astigmatism develops from the attempt to compensate.

Apertures

Because the aperture sizes used in these experiments are still larger than the pupil size (typically 2 mm in diameter) any effects of aperture size must be considered to be a function of reduced field size rather than a reduction in blur circle diameter. This would suggest that the control mechanism involves some sort of integration over retinal area. The critical angle is estimated to be <70 deg, the angular subtense at the cornea of the 10 mm aperture, since compensation is complete for this aperture size. Compensation is $<100\%$ for the 5 mm aperture which corresponds to an angular subtense at the cornea of 40 deg. Therefore the critical angle would be also expected to be >40 deg. Although decreased aperture size with plano lenses produces increased amounts of myopia and increased variability, the change is not a linear progression toward the refractive errors produced by form deprivation (Fig. 2). This would suggest that the emmetropization mechanism is at least partially functional even for small field sizes. The convergence of the data for +10 and −10 D lenses towards that of plano lenses, with smaller apertures, indicates that the effect of aperture size is not merely a function of more of the field receiving form deprivation from the translucent portion of the goggle. If this were the case we might expect to see a shift in the myopic direction of equal magnitude for all lens treatments. The observed values for the 2.5 mm aperture and −10 D lenses are in fact less myopic than those for the 5.0 mm apertures. The values for the +10 D lenses tend to be more myopic for 2.5 mm apertures than would be expected based on increased form deprivation. It would seem then that there is a real effect of aperture size superimposed upon form deprivation myopia created by the transluent portion of the lens–goggle system.

Although there is a progressive increase in myopia with smaller apertures, even the smallest aperture does not result in myopia of the magnitude produced by form deprivation; nor is the progression of myopia with decreased aperture size towards that of form deprivation linear. Even a small aperture seems to over-ride the form deprivation mechanism. Form vision to a relatively small retinal area is sufficient to control eye growth in the region of the eye that receives the normal vision, albeit less accurately than when larger areas are stimulated (Fig. 2). No attempt to evaluate the eye growth outside the area which received normal vision was made. The increase in myopia with decreased aperture size may be a result of local peripheral deprivation effects influencing the central region.

The changes seen with the slit apertures cannot be explained on the basis of an overall reduction in area. If this were the case values higher than those measures would have been expected. Further, astigmatism generally does not result when circular apertures are used but does so in about half of the birds when slit apertures are used. The inconsistency of the development of astigmatism and the lack of coincidence of the axis of astigmatism with the axis of the slit argues against an independent effect of aperture size on each meridian. It appears that astigmatism simply results when the eye is presented with a deprivation condition with which it cannot cope. Observations from the reversal experiments of Irving *et al.* (1992) also support this conclusion. The use of non-circular apertures results in an increase in variability with some birds showing an error in sign. The changes in the variability of the data suggest that this experimental manipulation interferes with the cues that the eye used to control its growth. The eye can no longer accurately determine the magnitude or the direction in which to grow and growth becomes more random.

The developing chick eye appears to be able to respond to defocus better when the aperture is circular. This could implicate asymmetrical optical aberrations such as off-axis astigmatism and coma in the determination of eye growth, particularly the direction. However, little is known about these aberrations in the bird eye. Further, the off-axis aberrations will be negligible in relation to the magnitude of the defocus used in these experiments.

Choroid

A possible explanation for differences in the speed at which hyperopia and myopia can be produced can be found in the asymmetries of the choroidal effect. A significant change in the thickness of the choroid is only found with convex inducing lenses and recovery from myopia. A significant decrease in choroidal thickness with concave inducing lenses or recovery from hyperopia is not apparent. The apparent asymmetry of the choroidal effect may simply reflect the fact that the choroid has a minimum thickness. In recovery from hyperopia and production of myopia the choroid cannot get any thinner. It is important to note that the choroidal changes described in this context are only temporary in nature. When the ocular growth mechanism takes over the choroid returns to normal. Thus, we assume choroidal effects could only operate to make the eye shorter, not longer. Assuming that choroidal changes can occur much

more rapidly than axial length growth (Wallman, Xu, Wildsoet, Krebs, Gottlieb, Marran & Nickla, 1992), production of hyperopia and recovery from myopia would be expected to be faster than production of myopia and recovery from hyperopia which do not involve the choroid. The choroidal effects need not result from an active choroidal process, although that is a possibility. For example if myopia were at least in part the result of stretching of the globe due to increased production of fluid, presumably liquid vitreous (Pickett-Seltner *et al.*, 1988), it would be possible for the eye to shrink if fluid was re-absorbed. It could conceivably be possible for re-absorption of fluid to occur during the production of lens induced hyperopia. The choroid would be a possible site for re-absorbed fluid to accumulate. This would of course increase choroidal thickness. The refractive effect of the increased choroidal thickness would result from the fact that it is easier for the choroid to displace the retina anteriorly than to displace the sclera posteriorly.

Magnification and the Stiles–Crawford effect

The two major effects of the lenses are blur and magnification. The blur circle diameters as determined by geometrical optics are a likely source of information as to the magnitude of the defocus but provide no information as to the sign. Since convex lenses produce magnification and concave lenses produce minification it is possible that this cue is used by the eye to determine the sign. However, the eyes are believed to respond independently to deprivation and it is difficult to imagine how the eye could determine whether an object had been magnified without some reference point; presumably the other eye. One possibility is the effect that magnification has on the Stiles–Crawford function. Magnification makes the function flatter (Lakshminarayanan, Bailey & Enoch, 1993) and this could be translated at the retinal level as a difference between convex and concave blur.

If the Stiles–Crawford effect were to be used to determine the sign of the defocus one would expect the response to be more robust to high powers and large apertures since the directional differences of the peripheral light rays between hyperopic and myopic defocus are greater under these conditions. The response to spherical defocus has been found to be equally robust to 5 and 10 D of defocus (Irving *et al.*, 1992). However, a decrease in response with aperture size is observed even though the smallest aperture used is still larger than the pupil. Therefore, these data do not support or rule out a role for the Stiles–Crawford effect in the determination of the sign of the defocus.

CONCLUSIONS

(1) During early development the chick eye can respond to both concave and convex astigmatic defocus. Myopia is most easily produced and hyperopia least easily produced along a meridian 135 deg from the palpebral fissure.
(2) Aperture size, shape and interruption of defocus can affect the refractive development of the hatchling chick eye. The compensation for refractive defocus becomes increasingly inaccurate with decreased aperture size, non-circular shape and brief periods of defocus interruption.
(3) The results for the aperture size experiments suggest that deprivation myopia and defocus induced refractive errors are not identical processes.
(4) Changes in choroidal thickness may be responsible for the faster rate of production of hyperopia and recovery from myopia.

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